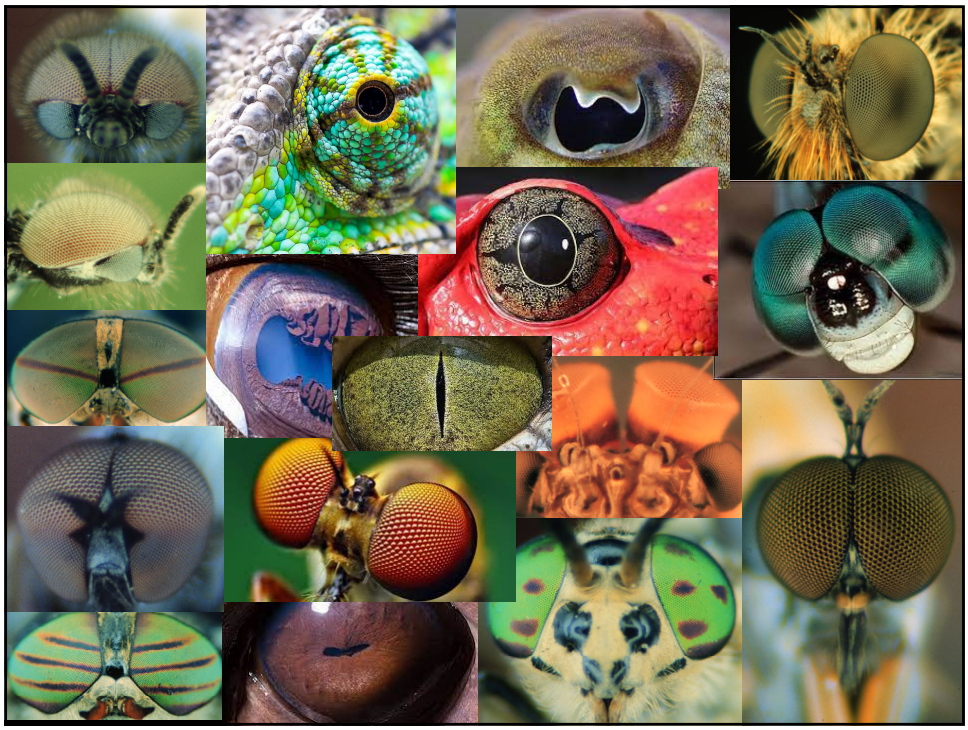
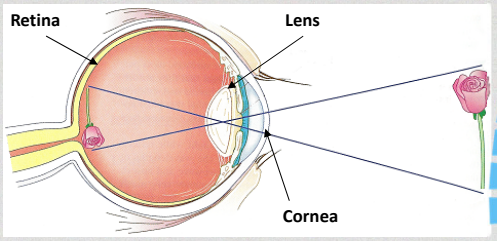


1

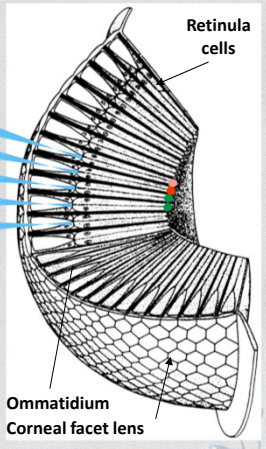
What makes a good eye?

A lens eye



Lens eyes:
- Vertebrates
- Molluscs
- Spiders

A compound eye



Compound eyes:
- Insects
- Crustaceans
- Polychaete Worms

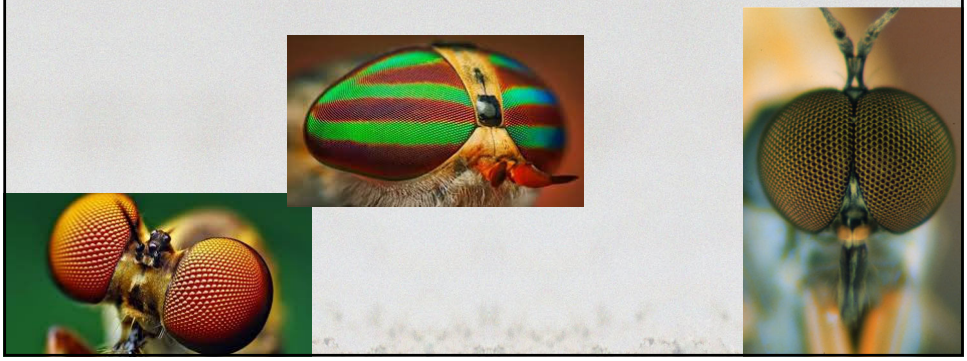
After Beatty 1995; Wehner 1981

2

Neural tissue is the most costly

The human brain uses 20% of oxygen, but weights only 2% of the body!

This cost and the cost of real estate (eye size), drives the diversity of eye evolution



3

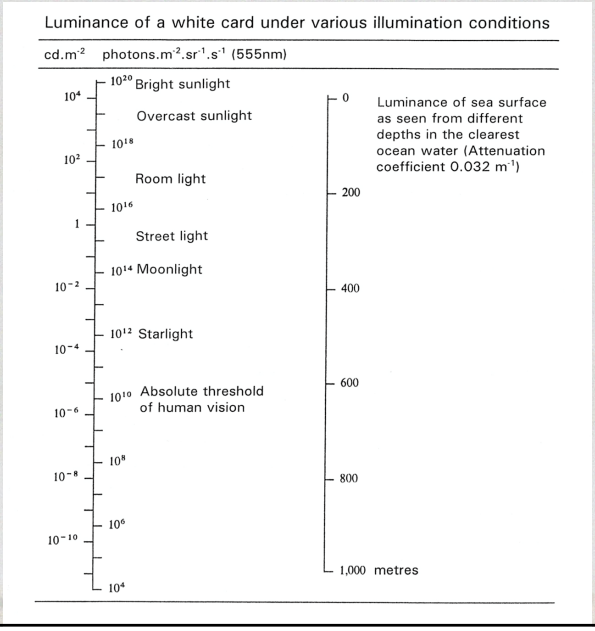
The working range of vision:

Starlight is
100 million times dimmer
than sunlight

Courtesy of Eric Warrant

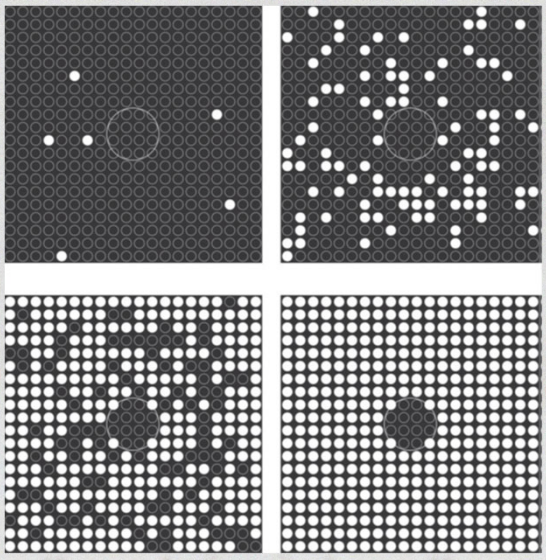
4

The working range of vision:



5

Photon capture / object detection



The central disk can only be reliably detected when light levels reach 100 – 1000x the threshold intensity

Pirenne (1967) in Land and Nilsson (2002)

6

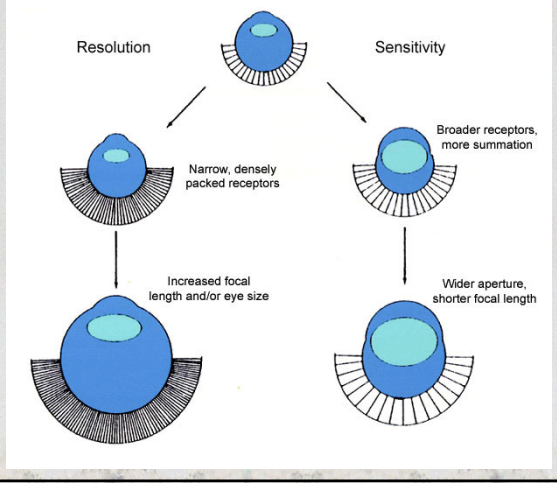
Photon capture / object detection

7

Trade offs: Resolution vs sensitivity

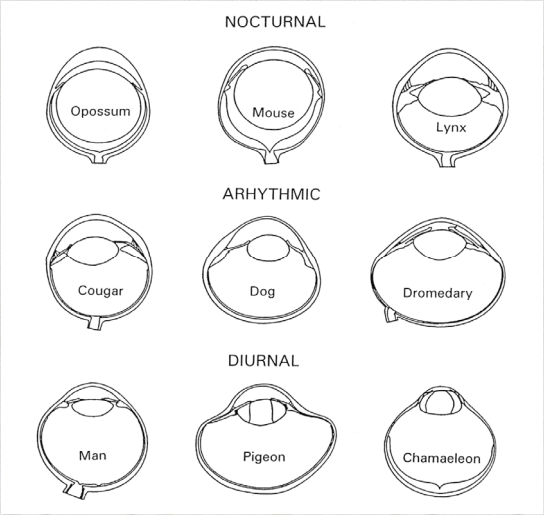
eye space is limited!

→ light sensitivity & spatial resolution are traded off in all eyes! Colour vision, polarisation vision make things worse



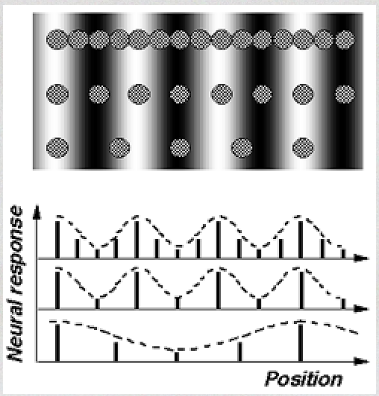
8

Trade offs: Vertebrate eye shape



9

Spatial resolution 1: Sampling resolution



The effectiveness of sampling arrays of different densities in reconstructing the viewed grating

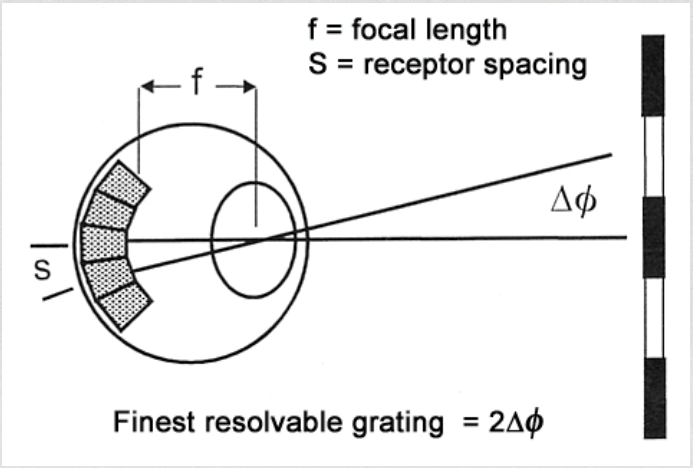
Nyquist limit (2 sensors per stimulus cycle (1 dark and 1 white bar)

Nyquist limit

Undersampling leads to aliasing (distortion)

10

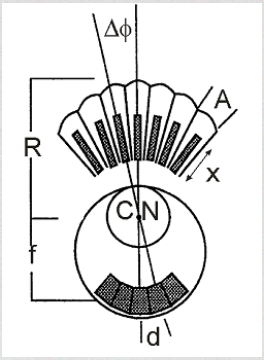
Resolving power



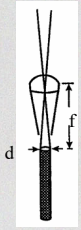
11

Spatial resolution 1: Sampling resolution

Compound eye



Lens eye



$\Delta\rho$ = d/f [radians]
[degrees = 180/π radians]

Inter-ommatidial angle $\Delta\phi$: (sampling resolution)
$\Delta\phi$ = A/R (= d/f in lens eye) [radians]

Acceptance angle $\Delta\phi$: (optical resolution)
$\Delta\rho$ = d/f [radians]

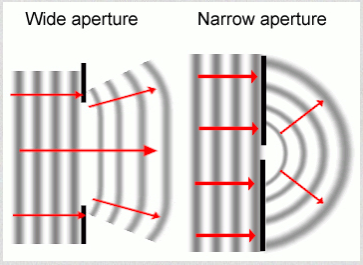
with:
A: diameter of the lens
d: diameter of the receptor
f: focal length of the lens
x: length of the receptor (rhabdom)
R: radius of the eye
C: centre of radius
N: nodal point of the lens

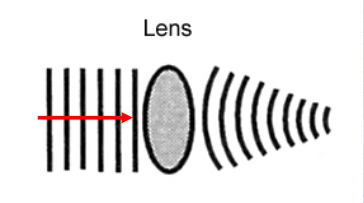
Eyes with **high sampling resolution** are **large**, have small **lenses (A)**, narrow **receptors (d)** and a **long focal length (f)**
(however, small lenses produce blur (see optical resolution - yet anther conflict)

12

Diffraction

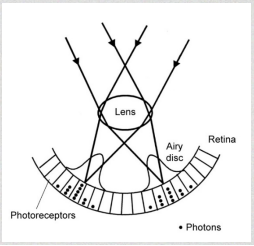
- **Even a perfect lens-based optical system cannot produce a point image of a point source**
- **Optical systems are often limited by diffraction**
- **Diffraction is the bending of light around an object**
- **Diffraction is wavelength dependent**
- **Big apertures diffract light less than small apertures (e.g. pupils)**
- **Light is diffracted by lenses - rays travelling through the centre of the lens are slowed more than peripheral rays**





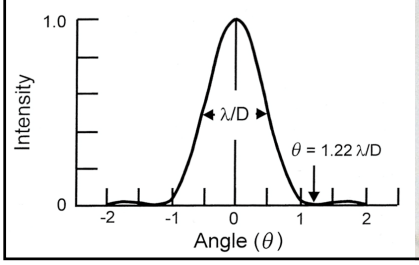
13

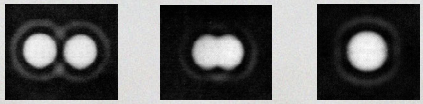
Spatial resolution 2: Optical resolution measures optical quality of the eye

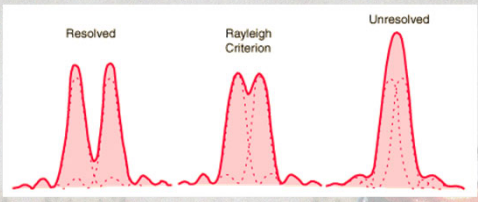


- Rayleigh criterion → minimum separable angle (Δθ) of the eye
- Wider apertures (D) give better ('optical resolution') - the ability to perceive two points of light as distinct entities (if allowed by sampling resolution)

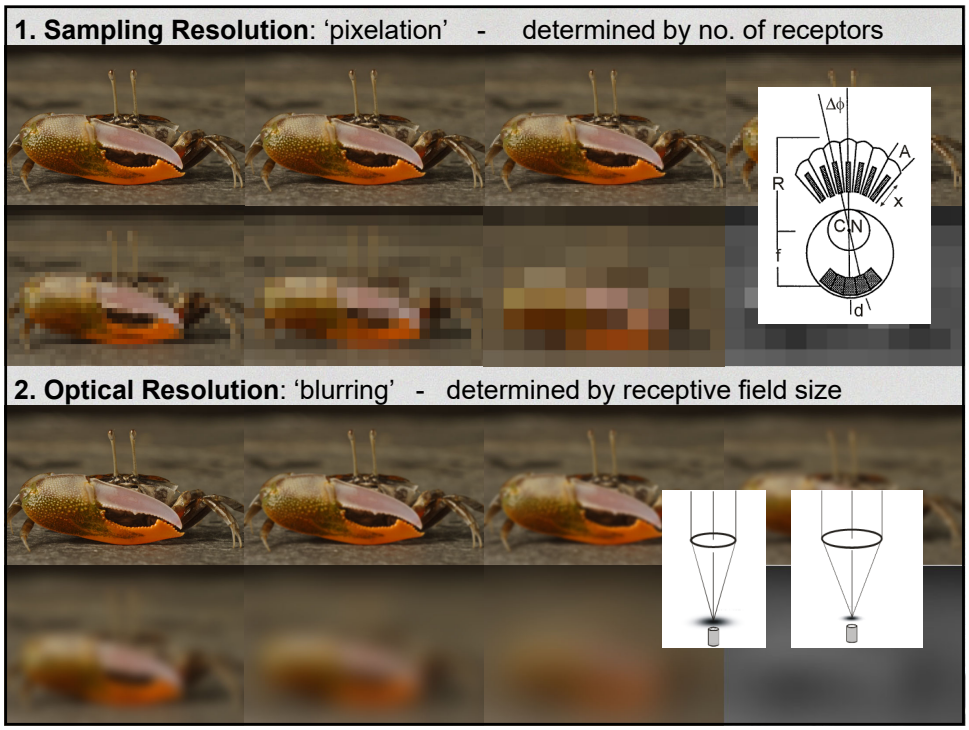
$$RayleighCriterion: \sin\Delta\theta \approx \Delta\theta = \frac{1.22 \cdot \lambda}{D}$$



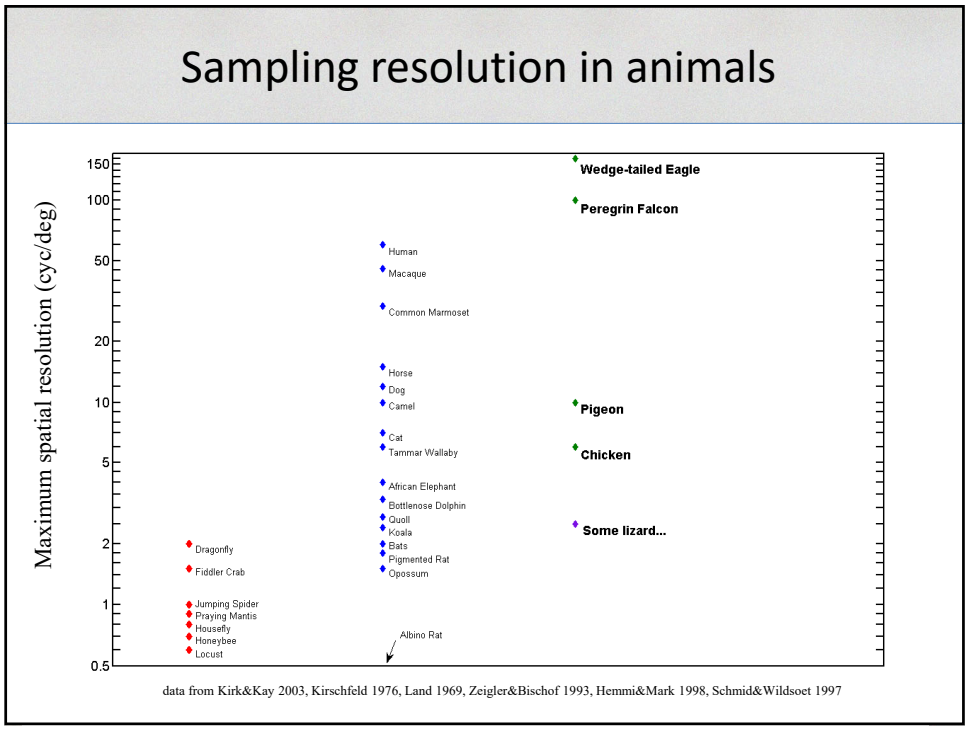




14

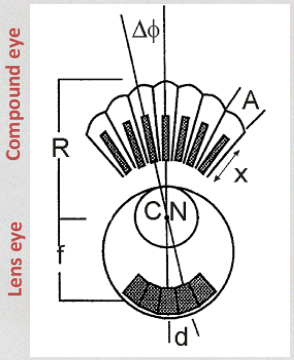

1. Sampling Resolution: 'pixelation' - determined by no. of receptors
Δφ
A
R
x
C.N
f
d
2. Optical Resolution: 'blurring' - determined by receptive field size

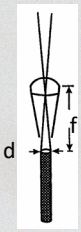
15


Sampling resolution in animals
Maximum spatial resolution (cyc/deg)
150
100
50
20
10
5
2
1
0.5
Wedge-tailed Eagle
Peregrin Falcon
Human
Macaque
Common Marmoset
Horse
Dog
Camel
Pigeon
Cat
Tammar Wallaby
Chicken
African Elephant
Bottlenose Dolphin
Quoll
Koala
Some lizard...
Bats
Pigmented Rat
Opossum
Dragonfly
Fiddler Crab
Jumping Spider
Praying Mantis
Housefly
Honeybee
Locust
Albino Rat
data from Kirk&Kay 2003, Kirschfeld 1976, Land 1969, Zeigler&Bischof 1993, Hemmi&Mark 1998, Schmid&Wildsoet 1997

16

What determines light sensitivity?





$\Delta\rho$ = d/f [radians]
[degrees = 180/π radians]

The fraction S of photons emitted by a surface which is absorbed by the visual pigment in a photoreceptor depends on:

$$S = (\pi/4)^2 A^2 (d/f)^2 \; kx/(2.3 + kx)$$

with:

A: diameter of the lens
d: diameter of the receptor
f: focal length of the lens
x: length of the receptor (rhabdom)
k: absorption coefficient
R: radius of compound eye
C: centre of radius of compound eye
N: nodal point of the lens in lens eye
$\Delta\rho$: acceptance angle

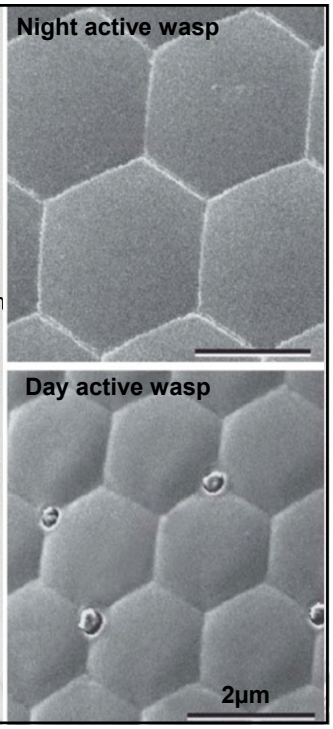
Eyes with **high light sensitivity** are **large**, have **large lenses (A)**, **long receptors (x)** with **large diameter (d)** and a **short focal length (f)**

17

Sensitivity enhancements

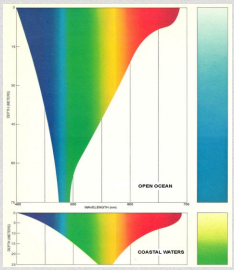
Adaptations to increase photon capture:

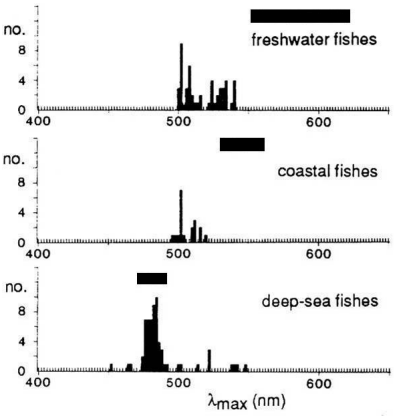
- Increased pupil/lens size
- Increased outer segment length and diameter
- Visual pigments matched to spectral environmen
- Reflective tapeta
- Grouped photoreceptors
- Tiered photoreceptors
- Retinomotor movements
- Superposition eyes (structural and neural)



18

Matched visual pigments

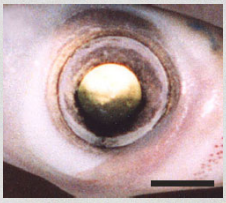




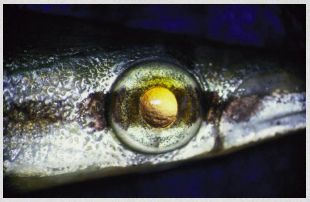
Histograms of λ_{max} values of rod visual pigments measured by microspectrophotometry of fishes from three habitats. The horizontal bars indicate the possible range of visual pigments most likely to confer maximum sensitivity in the different water types (after Lythgoe, 1988). Only the deep-sea fishes have rods best positioned to maximize photon catch. (Data mainly from Partridge *et al.*, 1988, 1989; Levine & MacNichol, 1979; Loew & Lythgoe, 1978.) (Figure from Partridge, 1990)

19

Reflective Tapeta

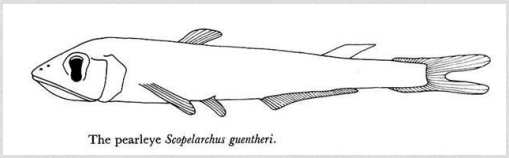


- Responsible for characteristic eye-shine in fish, mammals, invertebrates, etc...
- Tapetum reflects light not absorbed by the photoreceptors back onto the retina
- Increases optical sensitivity of the eye

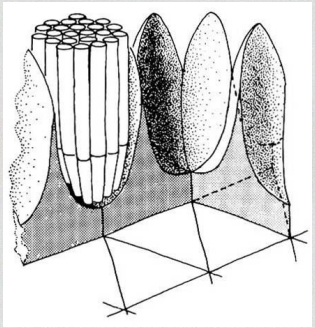


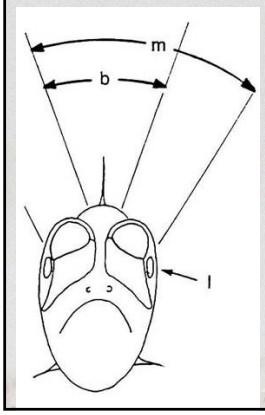
20

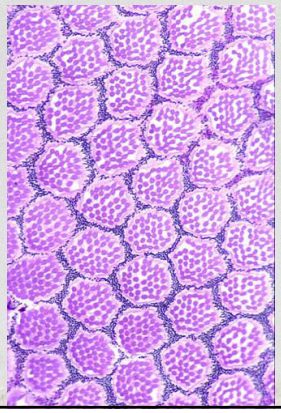
Grouped Photoreceptors



The pearleye *Scopelarchus guentheri*.



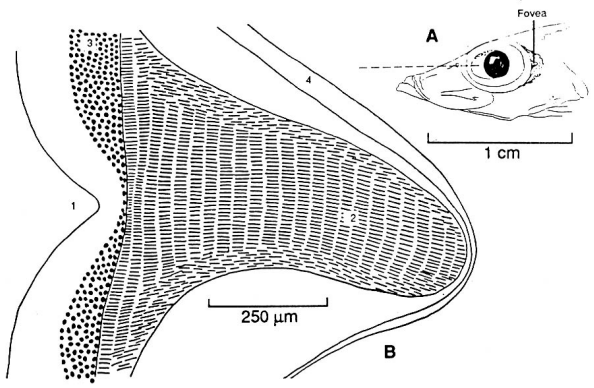




- Bundled photoreceptors
- Unique to teleosts from turbid / deep-sea habitats
- Tapeta in pit walls
- Optical isolation from adjacent pits
- Electrically coupled → summation

21

Tiered photoreceptors



Bajacalifornia drakei. (A) Head with the tissues behind the eye cut away to show the location of the fovea. The axes through the centre of the lens and the foveas cross in front of the fish. (B) Fovea diagram. There is a steep-sided pit, 1, in the retina, lined by radial fibre. The fovea externa, 2, contains up to 28 banks of ellipsoid-outer-segment complexes, compared with one or two poorly defined banks in peripheral retina. Rod nuclei, 3 are piled up in the foveal shoulders. The sclera, 4, is displaced outwards by the fovea externa (from Locket, 1985).

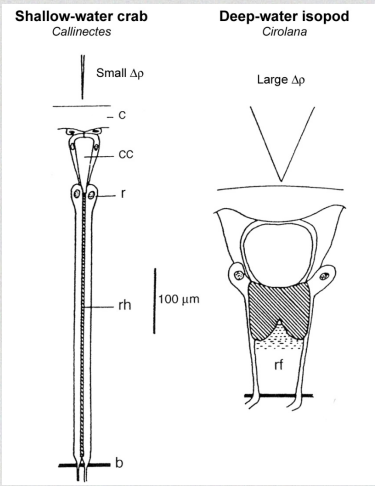
22

Main Concepts: What makes a good eye?

- Light sensitivity & spatial resolution are traded off (colour vision too as it requires several types of receptors)
- Large eyes are almost always better:
  - Long focal length (low minimum resolvable angle)
  - Wide aperture
    - reduced diffraction
    - more light
- Eyes with high spatial resolution are large, have large lenses (aperture), **narrow receptors and a long focal length**
- Eyes with high sensitivity are large, have large lenses (aperture), **long receptors with large diameter and a short focal length**

23

Trade offs: shape of ommatidia



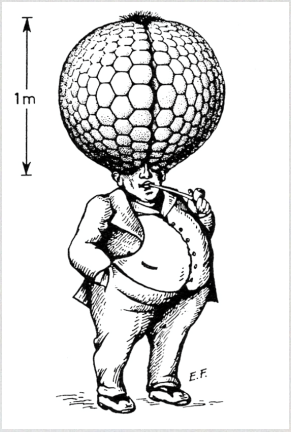
In all eyes there is a trade-off between resolution and sensitivity

Wider receptors have bigger Δρ and catch more light, but at the cost of resolving power

- Cirolana Δρ = 47° (0.02 cycles deg-1)
- Callinectes Δρ = 2° (0.5 cycles deg-1)
- Cirolana is ~4000x more sensitive

24

Compound eye resolution is limited by aperture size!



Compound eyes have poor resolution compared to camera-type lens eyes:

- 25µm diam. facet → 1° (1 cycles/deg)
- 2mm diam. pupil → 0.014° (70 cycles/deg)

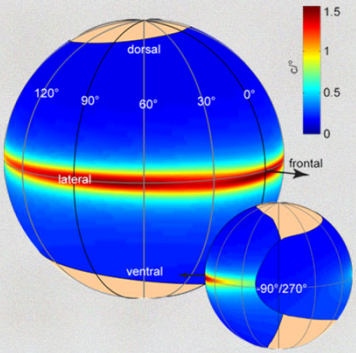
To have the same resolution as our camera-type eye, humans would need a compound eye 1m in diameter

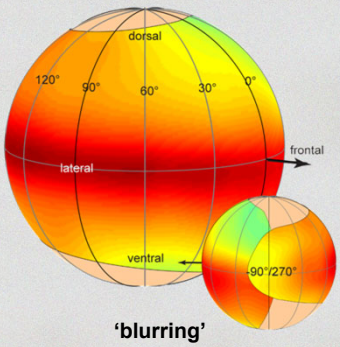
Compound eyes → smaller lenses (aperture) → lower resolution
Camera-type lens eyes → wider aperture → higher resolution

25

Resolution across visual space *U. vomeris*

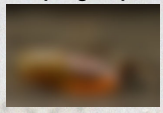
'pixelation'
Sampling resolution (vertical)



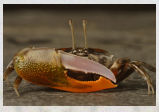


'blurring'
Optical resolution

sampling > optical



matched



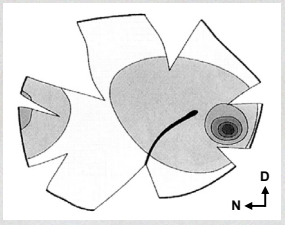
"undersampling"
optical > sampling

Smolka & Hemmi (2009)

26

Resolution across visual space: retinal topography

Area centralis

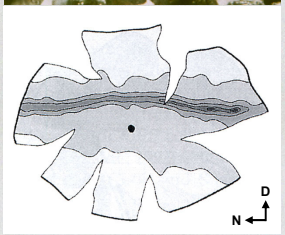


Coral cod

(Cephalopholis miniatus)

Coral reefs

Visual streak



Small-spotted dogfish

(Scyliorhinus canicula)

Benthic / mid-water

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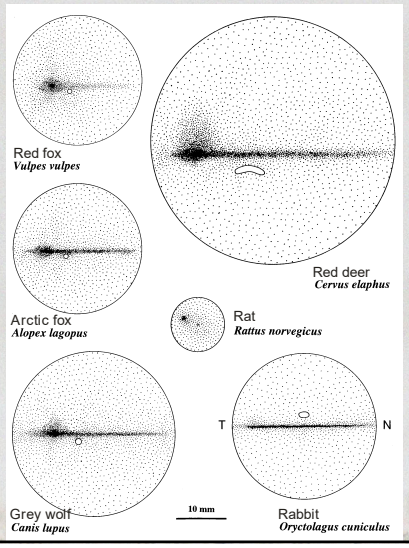
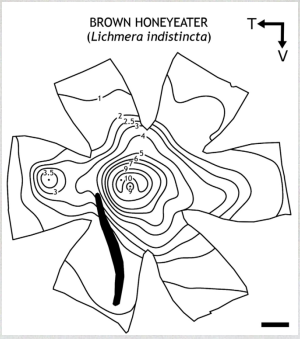
Spatial resolution: distribution of vertebrate ganglion cell densities

Animals living in flat worlds



An example of an animal living in a more complex (3D) environment



Coimbra et al 2014

Courtesy of Leo Peichl

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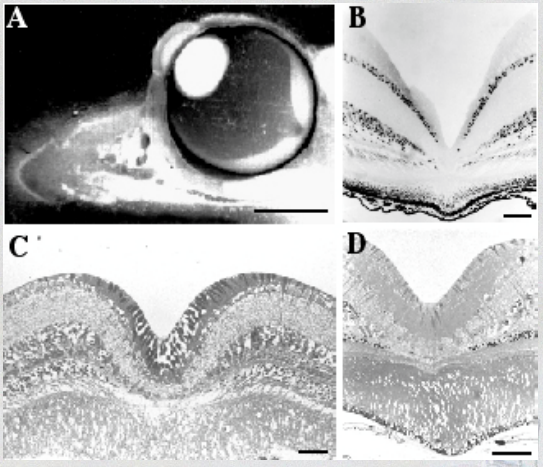
Fovea: sandlance

Indentation of the retina

Associated with increased photoreceptor cell density

Functions:

- Image magnification
- Motion detection
- Object fixation



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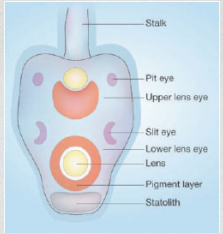
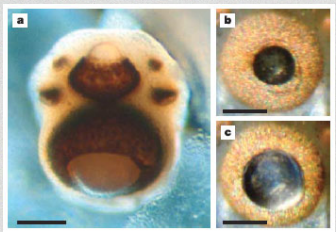
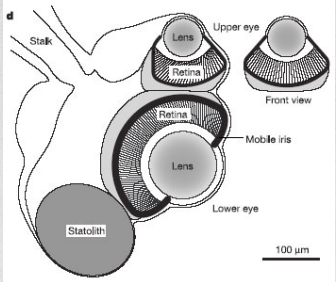
Cubozoans (box jellyfish)







Active swimming behaviour

Rhopalium or 'sensory club'

6 eyes:

- 2 lens eyes
- 4 pigment pit eyes

Lenses have graded RI

Mobile pupil

Single visual pigment → no colour vision?

Retina too close to lens for focused image

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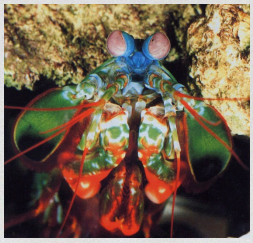
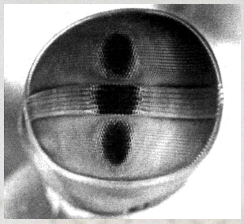
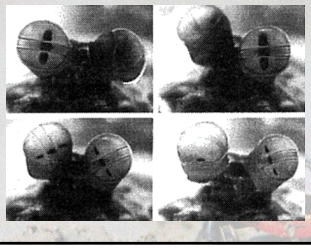
Stomatopods



- Apposition compound eye
- Linear area or 'midband' of specialised ommatidia designed for colour and polarization vision
- 16 visual pigments, coloured filters → colour vision
- 3 visual areas view same region of space!





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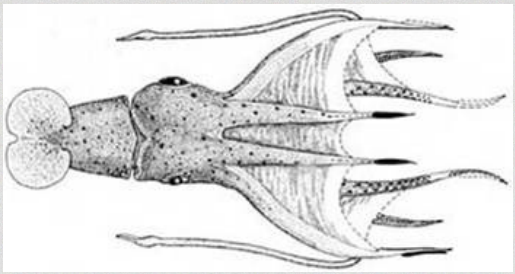
Mid-water squid *Histioteuthis*



Right eye:

- Larger
- Yellow lens
- Tubular, narrow field of view
- Looks upwards to detect prey against downwelling light

Left eye:

- Smaller
- Clear lens
- Wide field of view
- Looks downwards, perhaps to detect predators

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